The RIVER MASTERS

Hippos are the nutrient kingpins of Africa's waterways

By **Elizabeth Pennisi**, *at the Mpala Research Centre in Kenya*

In the cool, early morning light, the hippos are at peace. Just the tops of their massive heads are above the water, mist streaming from their nostrils as they exhale. One rests its chin on a rock. Another wiggles its ears and then gently submerges, leaving a circle of expanding ripples. A third yawns, exposing four large canines, muscular lips, and a giant, bright pink mouth.

To ecologist Douglas McCauley, this scene on the Ewaso Ng'iro river in Kenya is far more than a safari postcard. Unseen, massive amounts of nutrients are entering the river, helping sustain the ecosystem: The hippos are pooping.

For the complex food webs of sub-Saharan Africa, hippo dung is an elixir. Just as salmon swim upstream in northern latitudes to spawn and die, infusing rivers with the stuff of life from their own decaying bodies, hippo dung transfers energy from land, where the animals graze, to Africa's turbid rivers, fueling growth of the organisms at the base of the food web. "We think of hippos as megaton salmon," says McCauley, of the University of California (UC), Santa Barbara. By measuring telltale ratios of carbon isotopes, McCauley, working with Justin Brashares, a conservation biologist at UC Berkeley, and others, has traced the flow of energy through the food web, from hippo dung on up to crayfish and barbel fish. Their studies have revealed that hippos transport so much carbon and other nutrients in their prodigious excrement that they can support—or poison—an entire aquatic ecosystem.

Researchers once shunned hippos in the wild, deeming the scientific payoff too small for the mortal risk of getting up close with the dangerous beasts. The extraordinary story of hippo poop is changing minds. "Up until now there's been a great deal of speculation and back-of-the-envelope calculations," says Robert Naiman, an ecologist emeritus at the University of Washington, Seattle. "Finally we have quantitative evaluations of the role of hippos," he says—and a case study of the powerful ecological role a single large animal can play.

PHOTO: E. PENNISI/SCIENCE

MCCAULEY'S TOUSLED SANDY HAIR contrasts sharply with the crisp white dress shirt he's wearing to avoid sunburn on the sun-drenched savanna. When he first encountered a hippo in the wild in 2002, he recalls, "I was scared to death." Ornery and territorial, these aquatic herbivores are considered by many to be Africa's deadliest animal, reputedly killing more people than elephants or lions. Weighing up to 4 tons, they can sprint as fast as a person, crushing victims to death with their powerful jaws or by trampling them. And although McCauley used to think he was safe on land when hippos are in the water, one day when he was sampling fish from the riverbank a hippo surfaced ever closer and then suddenly charged up the bank, forcing him to make a dash for his Land Cruiser.

Apart from their reputation for inflicting painful forms of death, relatively little is known about how hippos interact with each other, with other creatures, and with the environment. "It seems like at this point we shouldn't be at this square-oneish level, but with hippos we really still are," complains

Simply by eating and excreting, the hippopotamus can transform entire African ecosystems.

Rebecca Lewison, a conservation biologist at San Diego State University in California and chair of the International Union for Conservation of Nature Hippo Specialist Group. "It's pathetic."

One reason for the dearth of knowledge is the acute challenge of telling one hippo from another. This close relative of cetaceans, McCauley says, is like "a cross between a baleen whale and a pig"—two well-studied species. But whereas biologists can distinguish individual whales by fin and tail markings, they have struggled to work out whether hippo ears, for example, have unique outlines, or whether individuals can be identified from scarring patterns, face color, or whisker placement.

PODCAST

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Merely observing the beasts is a challenge because they pass their days submerged in lakes, ponds, and eddies in muddy rivers. At dusk, they "swim" by bouncing off the river bottom and eventually clamber ashore. They graze in grassy "glades" at night—when snakes, elephants, lions, and hyenas make it unwise for a researcher to be out—and slip back into the water just before dawn. Nor can researchers easily fit them with the GPS collars used to track many kinds of African mammals for behavioral studies. Most collars slip right off a hippo, which doesn't really have a neck.

Last year, Tristan Nuñez, a graduate student at UC Berkeley, came up with an alternative strategy for tracking hippos. He took aim at basking hippos with his crossbow—but instead of arrows he fired barbed GPS tags of the sort used to track whales. It was hard to get a clean shot, he says, but twice he stuck a tag in a hippo's tough hide. Being able to track an individual hippo's movements was "a major triumph," Lewison says. But for now, McCauley says, "we don't have a sense of their patterns of movements," such as how far they wander at night for food.

To get answers, McCauley more than once climbed a tree overhanging a hippo pool and spent the day taking notes. And in 2012, he and Mordecai Ogada, now with the Laikipia Wildlife Forum in Nanyuki, Kenya, and their colleagues used camera traps to collect 50,000 hours of footage of hippo grazing areas. The team also drove 9 hours on a treacherous highway to Kenya's Mzima Springs, where clear water allowed them to observe hippos underwater both from the bank and from a partially submerged observation room for tourists. "They are quite comical … and graceful for being so big," says McCauley, who gained a new appreciation for the hippo ballerinas in the movie *Fantasia*. At Mzima, they watched young hippos romp like 2-year-old children and adult males establish dominance by spraying dung in the face of rivals.

TO PROBE THE ROLE hippos play in the savanna ecosystem, McCauley and his colleagues also established five sets of 30-square-meter plots, monitored by cameras, along the Ewaso Ng'iro river. Some plots are edged with evenly spaced poles that are just the right size to keep out hippos while allowing other animals through. Electrified wiring around other plots excludes most animals, and some plots have no fence at all. Twice a year, McCauley's team surveys plants in the plots and clips leaves and scoops soil to analyze nutrient content.

The experiment has revealed that hippos reshape the grasslands to their advantage. In plots they frequent, grass is stubbier and leafier because of repeated cropping. That's good for hippos, McCauley says: "Getting more leaf area per bite is better because it's much more nutritious," he says. In hippo-free plots, grass is more strawlike and flowers more frequently.

Given that a single hippo eats about 40 kilograms of grass a night, McCauley wanted to know how the animals' daily perambulations transport nutrients such as carbon, phosphorus, and nitrogen through the environment. Past studies of nutrient transport in ecosystems have focused on physical forces such as runoff and on the influence of plants and microbes. "Animal

Douglas McCauley sets up a camera trap to snap photos of hippos as they graze at night.

behavior has been left on the sidelines," says David Post, a community ecologist at Yale University. "Yet animals can move [nutrients] faster than physical forces or even in a way that's counter to these forces," he says.

To quantify the nutrient flows in African ecosystems, McCauley and his colleagues turned to isotopic analyses. Different plant species have characteristic proportions of heavy and light carbon isotopes in their tissues. Each plant's isotopic ratio provides a marker for its carbon as it works its way through the food web. Researchers can also add tracer isotopes to food for more precisely measuring the energy transfer from organism to organism.

Tracer isotopic analysis has unraveled nutrient use in birds, pigs, and sheep, but its use in wild animals would be unprecedented, says Todd Dawson, a plant ecologist at UC Berkeley, who led the isotopic analyses for McCauley's team. First they tried out the technique with captive hippos at Disney World in Florida. They fed the hippos food with known isotopic compositions and tracers and confirmed that the excrement preserved the same signatures. Once they proved they could track energy flow in this way, they fed hippo dung to guppies. Unpublished results show that the guppies' isotopic ratios mirrored those of the dung.

Back in Kenya, the team determined isotopic ratios of local plants. Then they went hunting for hippo dung. "It's like an Easter egg hunt," McCauley says. "There's not much there, but that's the point—not a lot of dung winds up on the land."

What's more, hippos don't just poop. They swish their tails as they go, sending dung flying into the bushes. On one outing, McCauley visited two sites and spent 45 minutes before finding what he was looking for: fresh dung, still warm, splattered in the sand. He carefully wrapped the prize in aluminum foil to carry back to the Mpala Research Centre, an institute near Mount Kenya that serves as McCauley's home and workplace while in Kenya.

From isotopes in dung samples, his team has learned which plant species hippos like to eat, and how hippo grazing skews the species assemblage of a glade. Next they hope to track how eating habits vary between wet and dry years and between seasons, which would indicate how hippos influence land eco-systems over time.

They are also using the isotopes to follow the nutrient chain further: from hippo poop to the fish and insects it nurtures. Already they have discovered that its nutritional impact on an ecosystem "is very strongly regulated by what the river is doing," McCauley says. Where currents are swift and hippos are few, the dung makes little difference to the river's other inhabitants. But come dry season, lower water flow leads to pooling, and isotope studies of river creatures show a clear signature of hippo poop. McCauley says that even as few as a dozen hippos "will become a dominant contributor to the nutrient pool." The fish they tested are an important commercial species in some Kenyan lakes, he notes, suggesting that hippos "need to be recognized as a life force for the industry."

But researchers have also discovered that hippo dung can be too much of a good thing.

ALONG THE MARA RIVER, a key waterway that meanders through the Serengeti, some 4000 hippos are crowded into 155 kilometers of river. The throng has increased 15-fold in the past several decades, likely in part because hunting is now illegal. At the same time, the river's water quality has deteriorated. When Amanda Subalusky and her husband, Christopher Dutton, came to Africa in 2008 to investigate, they flagged deforestation as a major water despoiler. But to their surprise, water quality was poorest in protected areas, particularly when flows were low. The common factor appeared to be hippo habitat.

To probe further, Subalusky, now a Yale graduate student, and Dutton, who studies with Emma Rosi-Marshall at the Cary Institute of Ecosystem Studies in Millbrook, New York, paid a visit to the Milwaukee County Zoo, home to three hippos. Zookeepers drain the hippo pool daily, allowing Dutton and Subalusky to quantify the urine and feces produced each day and determine the amount of nitrogen, phosphorus, and carbon the hippos egested. Extrapolating to the Mara, they will report in an upcoming issue of *Freshwater Biology* that 4000 hippos would contribute more than 36 tons of feces a day.

The Mara can't always cope with such abundance. Subalusky and her colleagues have linked sudden pulses of water after heavy rainfalls with precipitous declines in dissolved oxygen and fish kills, most likely brought on when the current stirs up thick beds of decomposing dung on the river bottom. Her team will test that idea with a boat that was built by Platypus LLC, a spinoff from a Carnegie Mellon University robotics group. The vessel looks like a crocodile (on the hunch that hippos will steer clear), and it should allow them to measure pool depth and dung deposition before and after a flood. "It's a chance to see where ecosystem dynamics are really influenced by an animal," Subalusky says.

McCauley witnessed a similar phenomenon in southern Tanzania's Ruaha River Basin. Until the late 1990s, its waters flowed year-round. But increased irrigation demands for rice have reduced the flow, and the river now breaks up into pools much of the year. Some pools teem with 100 or so hippos, while others have none. In the hippo-clogged pools, nutrients from dung can set off an algal bloom, and as the

A Milwaukee zoo pool that went from clean to filthy in less than a day allowed Amanda Subalusky to measure nutrient content of hippo dung and urine.

PHOTOS: AMANDA SUBALUSKY (2)

Ecosystem engineers

Hippos change the savanna and its waters in many ways. They deepen pools, keep water well mixed, change the water's chemistry, erode banks, form new channels, create "lawns" of closely cropped grass, and energize the food web with their dung.

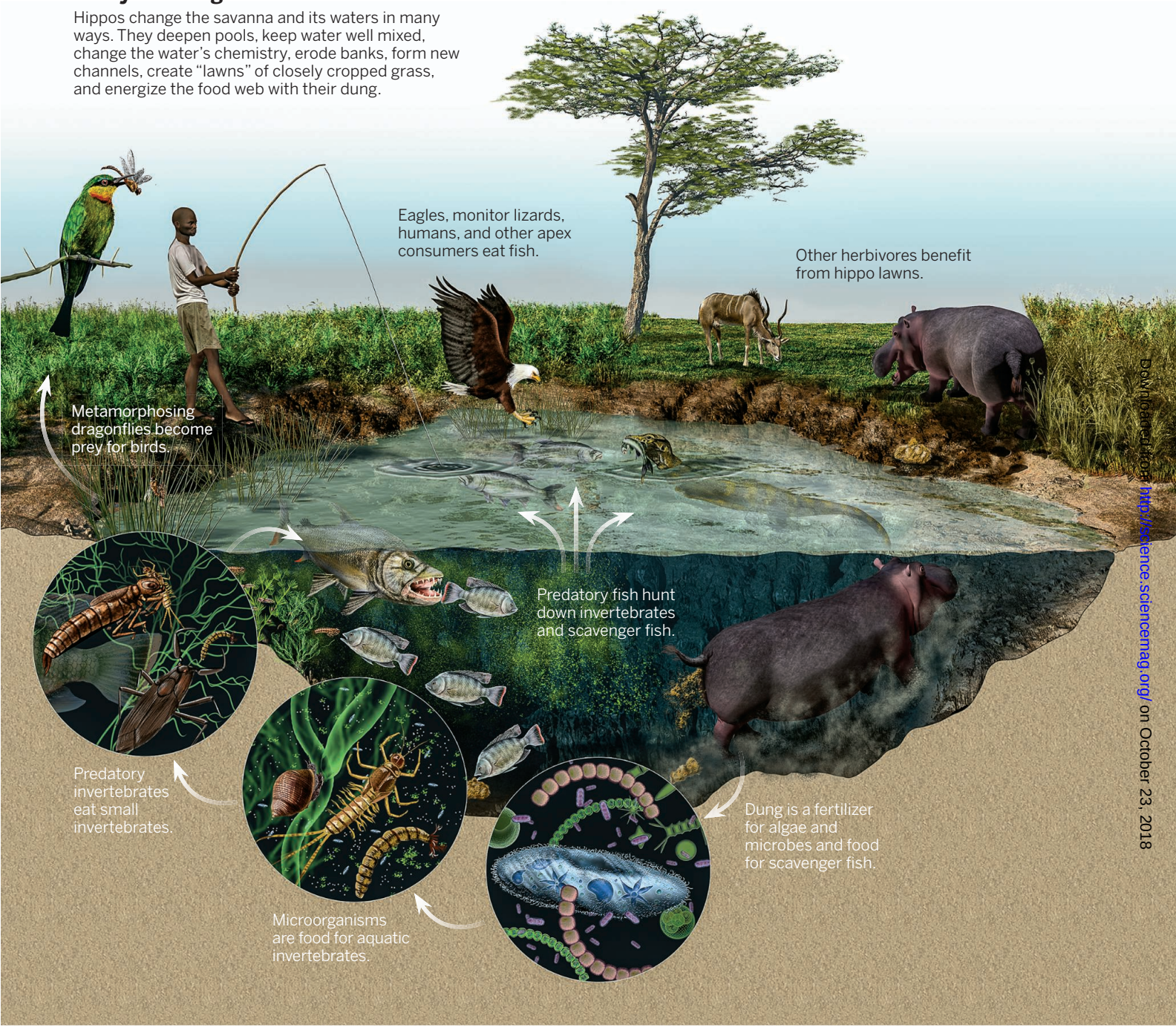

ILLUSTRATION: NICOLLE R. FULLER

dying algae sink and decompose, they draw down the oxygen, turning the water black. "There are few river animals that can cope with such conditions," McCauley says.

Despite their abundance in the Mara and Ruaha rivers, hippos broadly are on the decline. About 100,000 years ago, they roamed as far north as the United Kingdom and across much of Europe. They disappeared from Egypt a century ago, and now they are confined to sub-Saharan Africa. Even there they are threatened. In Mozambique, for example, relentless hunting and losses during the long civil war that ended there in 1992 reduced a population numbering in the thousands to just a few hundred. Today, an estimated 135,000 remain in all of Africa. Unlike elephants, which are also in steep decline, hippos "do not have a champion," says San Diego State University's Lewison.

The new portrait of the hippo as the unsung nutrient kingpin of sub-Saharan Africa suggests that as the animals decline, ecosystems will be transformed, affecting many other creatures. That prospect adds urgency to the efforts of the handful of scientists who are striving to paint a more nuanced picture of the formidable mammal. "Scientifically, we've overcome quite a few challenges," says UC Berkeley's Dawson. The next challenge, he says, is making the science relevant to conservation. ■

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